Int. J. Plant Sci. 173(3):239–250. 2012.
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1058-5893/2012/17303-0002$15.00 DOI: 10.1086/663965

LEAF ARCHITECTURE OF EXTANT SPECIES OF *ROSA* L. AND THE PALEOGENE SPECIES *ROSA LIGNITUM* HEER (ROSACEAE)

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Leaf fossils of *Rosa lignitum* Heer have often been documented as an accessory element in mixed mesophytic forests from the Oligocene and Miocene of central Europe. Its relationship to extant rose species is not yet firmly understood because leaf morphology contributes only marginally to the current taxonomy of the genus *Rosa* L. In this study, we investigate which extant rose species have structural leaf characters most similar to those of *R. lignitum* and whether the distribution and ecology of these extant species fit with the conditions hypothesized for the paleovegetation containing *R. lignitum*. Therefore, we examined the leaf characters of 32 extant rose species for their diagnostic value in taxonomy and compared these data with characters observed in *R. lignitum* from five Paleogene floras in central Europe. Most remarkably, we detected semicraspedodromous venation in *R. lignitum*. This venation pattern was found only in a few species of *Rosa* distributed in Southeast Asia, whereas the majority of extant rose species developed strictly craspedodromous venation. The distribution of extant species with semicraspedodromous venation in mixed broad-leaved deciduous and evergreen forests in subtropical China clearly corresponds to the hypothesized mixed mesophytic forests in the European paleovegetation. Thus, this study of detailed leaf morphology of *Rosa* again supports the previous assumption that the zonal vegetation of the central European Oligocene is partly comparable to extant forest types in Southeast Asia.

Keywords: Rosaceae, leaf venation, paleobotany, *Rosa lignitum*, Tertiary relict, fossil leaf.

Online enhancements: appendix tables.

Introduction

In angiosperms, morphological and anatomical leaf characters—especially leaf venation patterns—have been widely used to classify dicotyledonous macrofossils and to infer their next living relatives (Roth-Nebelsick et al. 2001). In numerous detailed studies comparing leaf architecture among fossil species from different strata with extant species, evolutionary trends of venation patterns within plant families and genera could be shown (Hickey and Wolfe 1975; Fuller and Hickey 2005; Taylor 2008). Some studies investigated leaf morphology and anatomy of fossils assigned to Rosaceae (Lis 1992; De Leon and Cevallos-Ferriz 2000; Erwin and Schorn 2000; DeVore and Pigg 2007), but leaf architecture found in fossil species of the genus *Rosa* compared with those of extant rose species has not been surveyed in detail yet.

In accordance with the present Northern Hemispheric distribution of the genus *Rosa*, fossil roses have been documented in North America, East Asia, and Europe from the Late Eocene to the Pliocene (Becker 1963; Kirchheimer 1973; DeVore and Pigg 2007). In some cases spiny twigs, odd-pinnate leaves, fruits, and sepals were found (Becker 1963; Kvaček and Walther 2004), but single leaflets are the most frequent remains in fossil floral assemblages. The often fragmentary preservation of fossils and their sometimes sparse description has cast doubts on the identification of a large number of fossil rose species as members of the genus *Rosa* (Kirchheimer 1973). In central Europe, the leaf morphospecies *Rosa lignitum* Heer (Heer 1869) has often been recognized in Oligocene and Miocene floras. Heer's original designation has been widely accepted in the paleobotanical literature (Bůžek et al. 1976). Mai and Walther (1978) regarded two features as crucial for the assignment of the fossil material to *Rosa*: the entire-margined base of the leaflet and the epidermal characters obtained from the cuticles, including anomocytic stomata with pronounced cuticular ledges and fine cuticular striation on the abaxial side. Recently, repeated co-occurrences of *R. lignitum* leaves and leaflets and *Rosa saxonica* (Engelhardt) Kvaček & Walther fruits provide additional evidence for the genus determination of the leaf fossils (Kvaček and Walther 2004; Walther and Kvaček 2007; fig. 1). These fruits and leaves most likely belong to the same fossil plant that could be regarded as one of the rare assembled whole-plant species of the genus (Kvaček and Walther 2004; Walther and Kvaček 2007). *Rosa lignitum* (including *Rosa bohemica* Engelhardt) has been found at several fossil sites in northern Bohemia (Czech

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Manuscript received May 2011; revised manuscript received October 2011.

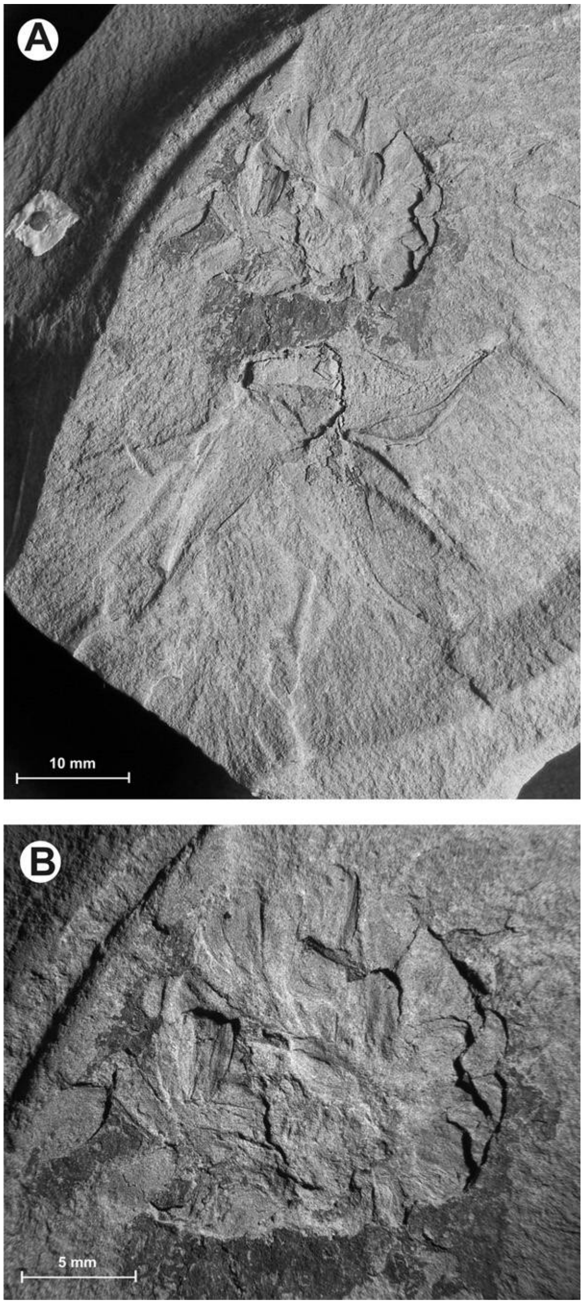

Fig. 1 Fossil fruit of *Rosa*: *Rosa saxonica* (Engelhardt) Kvaček & Walther, holotype of *Diospyros saxonicus* Engelhardt 1870: pl. 5, fig. 11, orig. Walther and Kvaček 2007: pl. 14, figs. 1–2, Seifhennersdorf (Saxony, Germany), Early Oligocene, MMG PB Sf 8283. *A*, Whole specimen. *B*, Detail showing impressions of fruitlets.

Republic) and Saxony (Germany) that are part of the Atlantic-Boreal province of central Europe (Mai 1995). This leaf morphospecies has been recognized as a common-accessory element of paleovegetation both in coastal lowlands and in uplands, including volcanic settings. These volcanic areas belong to the Ohře rift, which is a Paleogene to Neogene magmatic province in central Europe (Pfeiffer and Suhr 2008). Respective fossils have been found in the strata of the České Středhoří volcanic complex (northern Bohemia, Czech Republic), in particular at the sites of Bechlejovice (Kvaček and Walther 2004), Kundratice (Kvaček and Walther 1998), and Suletice-Berand (Kvaček and Walther 1995) and in the strata of Seifhennersdorf in eastern Saxony (Walther and Kvaček 2007) at the eastern margin of the Ohře rift. These floras in volcanic settings (volcanic floras sensu Kvaček and Walther 2001) were mostly accessed from lacustrine diatomite layers within volcanic rock series. By means of the K-Ar method, the volcanic rocks have been dated as Oligocene in age (Bellon et al. 1998). Except for the Suletice-Berand flora, all other volcanic floras mentioned herein belong to the middle Rupelian megafloral assemblage Seifhennersdorf-Kundratice (Kvaček and Walther 1998). The Suletice-Berand flora has been assigned to the slightly younger (latest Rupelian–early Chattian) assemblage Nerchau-Flörsheim (Kvaček and Walther 2001). *Rosa lignitum* has also been documented in the costal lowland megafloral assemblage Haselbach of the so-called Weißelsterbasin (central Germany; Mai and Walther 1978). The Haselbach horizon of the Böhlen Formation (Standke and Suhr 2008) consists of fluvial, lacustrine, estuarine, and brackish-marine sediments deposited in a costal floodplain (Kunzmann and Walther 2007). The lithostratigraphic age of this horizon is lowermost Oligocene (Standke et al. 2011) and thus corresponds with the ages of the above-mentioned volcanic floras (Mai and Walther 1978; Kvaček and Walther 2003). The Oligocene climate in central Europe was influenced by a global cooling after the Eocene-Oligocene boundary (Mai 1995; Tiffney and Manchester 2001; Mosbrugger et al. 2005). Paleoclimate changes resulted in a concurrent shift from subtropical–warm temperate, mostly evergreen vegetation in the late Eocene to warm temperate to temperate forests containing almost 40% deciduous woody plants in the Oligocene. These forests have been compared with modern mixed mesophytic forests, and all above-mentioned fossil sites are characterized by the occurrence of this vegetation type.

In contrast to fossil roses, extant species of the genus *Rosa* L. (Rosaceae) are mainly distributed in cold temperate regions of the Northern Hemisphere. A few species are found in warm temperate and subtropical regions, and *Rosa abyssinica* R.Br. ex Lindl. grows in the semiarid oreotropic regions of Ethiopia. The genus comprises ~200 species and has been traditionally divided into four subgenera, of which three are monotypic or have two species (subg. *Hulthemia* [Dumort.] Focke, *Hesperhodos* Cockerell, and *Platyrhodon* [Hurst] Rehder). The majority of species are placed in subg. *Rosa*, which has been divided into 10 sections (Rehder 1949; Wissemann 2003; Wissemann and Ritz 2005) on the basis of morphological characters of spines and fruits as well as variation of pinnation and persistence of sepals (Henker 2000). Although some species have characteristically shaped leaves, leaf morphology has not played a major role in rose taxonomy because many of the most easily measured leaf traits (e.g., number and size of leaflets) are also highly variable within species (Henker 2000; Reichert 2011). In contrast to *Rosa persica* Juss. (subg. *Hulthemia*), which has simple leaves, rose leaves are usually odd-pinnate and stipulate. Leaves are mostly deciduous, but the few species distributed in subtropical Southeast Asia (e.g., *Rosa banksiae* W. T. Aiton, *Rosa laevigata* Michx., and *Rosa bracteata* Wendl.)

and the Mediterranean area (e.g., *Rosa sempervirens* L.) are evergreen. The leaf margin is serrate to biserrate, but this can also vary within one individual (Henker 2000). In contrast, the presence of scenting glands on leaf surface and margins turned out to be a reliable character to circumscribe European species of sect. *Caninae* (DC.) Ser.

This study aims to hypothesize the next living relative of *R. lignitum* from distinct Paleogene floras in central Europe. Therefore, we evaluate morphological and anatomical leaf characters across extant species of the genus *Rosa* and compare them with the leaf architecture found in *R. lignitum*. Once we infer the most similar extant rose species, we discuss whether their ecology and biogeography coincide with paleoclimatic reconstructions for fossil floras containing *R. lignitum*.

Material and Methods

Plants of Extant Species

We investigated leaves of 32 extant rose species representing characteristic members of the subgenera and sections of *Rosa*. For each species we analyzed material from one herbarium specimen (app. A). Selection and terminology of leaf characters followed the *Manual of Leaf Architecture* (table 1; Leaf Architecture Working Group 1999). To determine shape, lower-order venation, and structure of margins, five leaflets were analyzed in detail by eye or with a microscope (Wild M3Z; Leica, Solms, Germany). Apex and base angles were measured from digital photographs with the help of Adobe Photoshop (ver. 6.0). Higher-order venation, presence of hairs and glands on leaflet surface and margin, and the anatomical structure of epidermal cells were analyzed in one to three leaflets. For this, leaflets were bleached and stained according to the following protocol. Dry leaflets from herbarium specimens were hydrated in distilled water with a drop of a conventional detergent at room temperature for 2–3 d and then bleached with chloral hydrate (>99.5%) at ~70°C for up to 6 h. After rinsing in distilled water, the leaflets were stained with safranin or methlylene blue (one drop of 0.5% staining solution in 15 mL of distilled water) for up to 30 min. Leaflets were examined under ×3.2–32 magnification using a Leitz Dialux 22 microscope (Leitz, Wetzlar, Germany) and photographed using a digital microscope (VHX-600; Keyence, Neu-Isenburg, Germany).

Fossil Plants

We investigated 129 leaves of *Rosa lignitum* (121 single leaflets and 8 incomplete preserved pinnate leaves) from five different localities in Germany and the Czech Republic (table B2 in the online edition of the *International Journal of Plant Sciences*). The collections are stored at the Senckenberg Natural History Collections Dresden, Paleobotany Section (acronym, MMG PB). The leaflets were identified as *R. lignitum* on the basis of laminar morphology and epidermal anatomy in previous publications describing the fossil floras of the respective sites (Mai and Walther 1978; Kvaček and Walther 1995, 1998, 2004; Walther and Kvaček 2007). Because of the differences in the quality of preservation of

Table 1

Characters of Leaf Morphology and Anatomy according to the Leaf Architecture Working Group (1999) Investigated in Herbarium Specimens of Extant Rose Species

Category	Investigated characters
Leaf morphology	No. leaflets[a]
	Laminar area of leaflet (mm^2)[a]
	Laminar shape[a]
	Laminar symmetry[a]
	Ratio of length to width of lamina (laminar L/W ratio)[a]
	Angle of base and apex of the lamina
	Shape of base and apex of the lamina[a]
	Type of leaf margin
	Presence of glands
	Presence of hairs
Venation	No. vein orders
	Category of primary veins[a]
	Category, spacing, and angle of secondary veins[a]
	Category, course, and angle variability of tertiary veins
	Category of fourth-order veins
	Category of fifth-order veins
	Areolation
	Category of freely ending ultimate veins (FEVs)
Leaf margin (teeth)	No. teeth orders[a]
	No. teeth/cm leaf margin[a]
	Shape of teeth
	Shape of tooth sinus
	Shape/presence of glands of tooth apex
Epidermis	Anatomy of stomata

[a] Also investigated in fossil rose leaves.

the leaves and leaflets, only a limited set of characters could be investigated (table 1). The fossils were examined using a Leica MZ APO stereomicroscope equipped with a digital camera (DFC 320). Digital images were processed with Corel PHOTO-PAINT X3 software.

Results

Extant Plants

We identified 12 constant characters for which we did not observe any variation among the investigated species (table 2). Stomata of all investigated specimens were surrounded by undifferentiated subsidiary cells (anomocytic). In some specimens stomata were sunken. All other leaf characters differed qualitatively or quantitatively between investigated specimens (table B1 in the online edition of the *International Journal of Plant Sciences*). We excluded the character "shape of teeth" from further analyses because it varied considerably within a specimen and even within a leaflet. Except for the simple leaves of *Rosa persica*, the number of leaflets ranged from three to 15. Most had elliptic laminae, but those of *Rosa stellata* Wooton and *Rosa willmottiae* Hemsl. were obovate. We observed asymmetrical leaflet bases in members of most sections but symmetrical bases in *Rosa laevigata*, *R. stellata*, and *R. persica* (fig. 2*A*, 2*B*). Roundish leaflets (ratio of length to width of lamina [laminar L/W ratio] of ≈1.5; fig. 2*C*) had rather obtuse apices and base angles (e.g., *Rosa micrantha* Sm.); angles were acute in rather elongate leaflets (laminar L/W ratio of ≥2; e.g., *Rosa banksiae*; fig. 2*D*). The apex was mostly convexly shaped; a retuse apex was observed, for example, in *Rosa laxa* Retz and sect. *Pimpinellifoliae* (DC.) Ser. (fig. 3*A*, 3*B*). Secondary veins terminated in teeth at the margin (craspedodromous; e.g., *Rosa sericea* Lindl.; fig. 3*D*) or branched into two ends, one terminating in a tooth and the other joining the next secondary vein (semicraspedodromous; e.g., *Rosa roxburghii* Tratt.; fig. 3*C*). The distance between secondary veins and their angle to the primary vein were mostly uniform, increasing or decreasing toward the base of leaflets (table B1). Tertiary veins connected the secondary veins discontinuously (alternate percurrent) or rejoined other tertiary or secondary veins randomly (random reticulate). We observed up to three orders of teeth at the leaf margin; the spacing of first-order teeth ranged from ~4 teeth/cm leaf margin (e.g., *Rosa wichurana* Crép.) to 10 teeth/cm leaf margin (e.g., *R. banksiae*). Tooth apices were either simple or glandular (fig. 3*E*, 3*F*). Hairs and glands were observed in ~50% of investigated samples.

Fossil Plants

Preservation of leaves and leaflets of *Rosa lignitum* allowed mainly gross morphological characters to be examined (fig. 4); venation of leaflets was not always recognizable (tables 3, B2). In three specimens of *R. lignitum* from the Seifhennersdorf site a semicraspedodromous pattern of secondary venation was observed that was also found in extant species, such as *R. banksiae*, *Rosa bracteata*, *Rosa helenae* Rehder & E. H. Wilson, and *R. roxburghii* (fig. 4*G*, 4*H*). Leaflets of *R. lignitum* were mostly elliptic with asymmetrical bases (fig. 4*C*, 4*E*) and rounded, convex, or straight-convex apices (table 3; fig. 4*B*, 4*E*). Their laminar L/W ratio was ~2, but we observed considerable variation between roundish leaflets with a laminar L/W ratio of ~1.3 (fig. 4*B*, 4*D*, 4*E*) and elongate leaflets with a laminar L/W ratio of 2.9 (table 3; fig. 4*A*, 4*C*, 4*F*). The leaf margin of *R. lignitum* was serrate, with mostly 4–5 teeth/cm leaf margin. In some cases two orders of teeth and a nontoothed basal third of the leaf margin were observed (fig. 4*H*).

Discussion

Morphological Characters of Rose Leaves

Of 31 investigated leaf characters, 19 varied among species, and some also varied within species (e.g., teeth shape; table B1). We observed no substantial variation between species in 12 characters (table 2). None of the investigated characters turned out to be a clear-cut diagnostic trait defining a subgeneric unit within *Rosa*, but we found combinations of several leaf traits that were typical for groups of species

Table 2

Constant Morphological and Anatomical Characters of Rose Leaves and Leaflets according to the Leaf Architecture Working Group (1999)

Character	Character state
Type of leaf margin	Serrate
No. vein orders	Five
Category of primary vein	Pinnate
Course of tertiary vein	Exmedially ramified
Angle of tertiary vein to primary vein	Obtuse
Category of forth-order veins	Regular polygonal reticulate
Category of fifth-order veins	Dichotomizing
Areolation	Well developed, five or more sided
Freely ending ultimate veins (FEVs)	Two or more branched
Tooth spacing	Regular
Shape of tooth sinus	Angular
Stomata type	Anomocytic

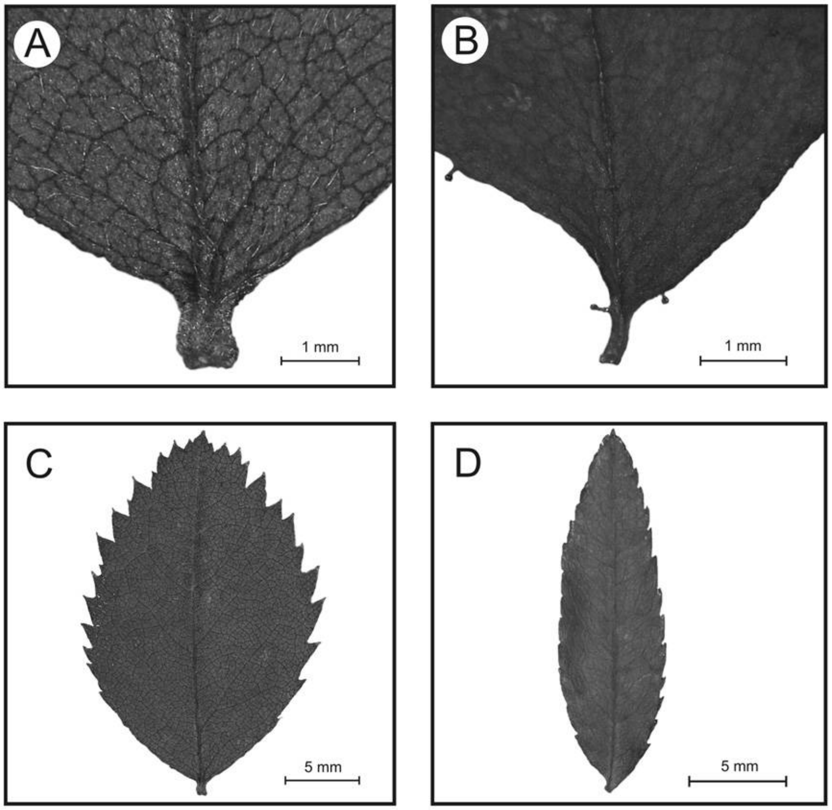

Fig. 2 Leaflet characters of extant species of the genus *Rosa*. *A*, Symmetric leaflet base of *Rosa micrantha*. *B*, Asymmetric leaflet base of *Rosa pendulina* L. *C*, Leaflet of *R. micrantha* with a ratio of length to width of lamina (laminar L/W ratio) of 1.5. *D*, Leaflet of *Rosa banksiae* with a laminar L/W ratio of 3.3.

(table B1). However, the present data do not, unfortunately, control for the presumed high level of intraspecific variation within some of the characters.

The size of leaflets was variable (table B1). Previous investigations showed that the laminar L/W ratio was more useful diagnostically than the laminar area on European wild rose species because the latter differed between flowering and nonflowering shoots and depended on the position of a leaflet within the pinnate leaf as well as on ecological factors, such as sun or water availability (Keller 1931; Nybom et al. 1996; Henker 2000; Reichert 2011). Leaflets were mostly elliptic or elliptic-oblong with rounded, convex, or cuneate bases. The shape of leaflets has been successfully used to discriminate European dogrose species (Nybom et al. 1997; Olsson et al. 2000), and the shape of the leaflet base is distinctive for species within sect. *Caninae* subsect. *Rubigineae* (Henker 2000). The number of teeth per 1 cm of leaf margin varied from four to 10, and it has been demonstrated that this trait does not vary substantially within species (Nybom et al. 1997). Contrary to this, we observed a high variation of tooth shapes even within a leaflet, which was also reported by Henker (2000) and Schulze (1996). Leaf venation architecture was similarly developed in all investigated species. Rose leaflets were always pinnate with a prominent primary vein and five vein orders, of which the fourth order formed regular polygonal areoles into which fifth-order veins branched dichotomously (fig. 3*E*). The general pattern of leaf architecture is probably genetically fixed and thus has often been applied for taxonomy of macrofossils (Roth-Nebelsick et al. 2001). However, some characters are influenced by environmental conditions; for example, the density of veins has been used as climate proxy (Uhl and Mosbrugger 1999).

We observed the most obvious variation in the category of secondary veins. The majority of species had craspedodromous secondary veins terminating in a tooth at the margin (fig. 3*D*). In a few species venation was semicraspedodromous (fig. 3*C*) because secondary veins branched at the margin, with one branch leading into a tooth and the other branch joining with the supra-adjacent secondary vein, forming a loop (Leaf Architecture Working Group 1999). Close relatives of *Rosa* from subfamily Rosoideae develop mostly craspedodromous venation (e.g., *Rubus* L., *Fragaria* L., and *Sanguisorba* L.). Semicraspedodromous venation is found in more distantly related genera; for example, in *Prunus L.* or in pinnately leaved species of *Sorbus* (Merrill 1978). The most conspicuous semicraspedodromous venation was detected in *Rosa banksiae*, *Rosa bracteata*, *Rosa helenae*, and *Rosa roxburghii* (intermediate states were observed in some species of sect. *Caninae*; table B1). Semicraspedodromous venation is presumably also typical for the so-called tea roses, including *Rosa chinensis* Jacq. and *Rosa odorata* (Andrews) Sweet (sect. *Indicae* Thory), because this venation is also found in modern Hybrid China roses, which originated by multiple hybridizations from these species (data not shown). Unfortunately, we

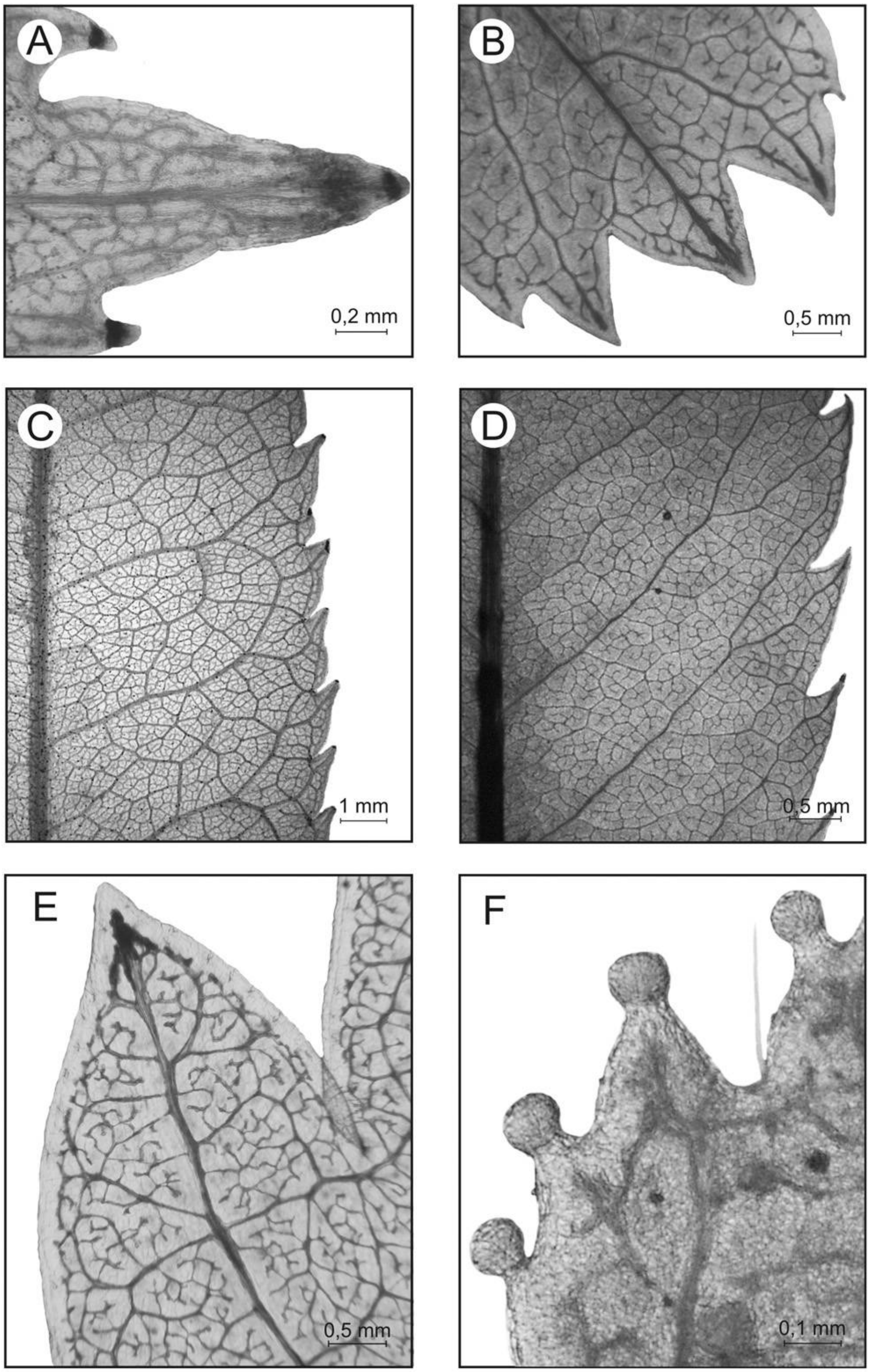

Fig. 3 Leaflet characters of extant species of the genus *Rosa*. *A*, Convex leaflet apex of *Rosa dumalis* Bechst. *B*, Retuse leaflet apex of *Rosa laxa*. *C*, Semicraspedodromous leaflet venation of *Rosa roxburghii*. *D*, Craspedodromous leaflet venation of *Rosa sericea*. *E*, Tooth at leaflet margin without glands of *Rosa glauca* Pourr. *F*, Tooth at leaflet margin with glands of *Rosa elliptica* Tratt.

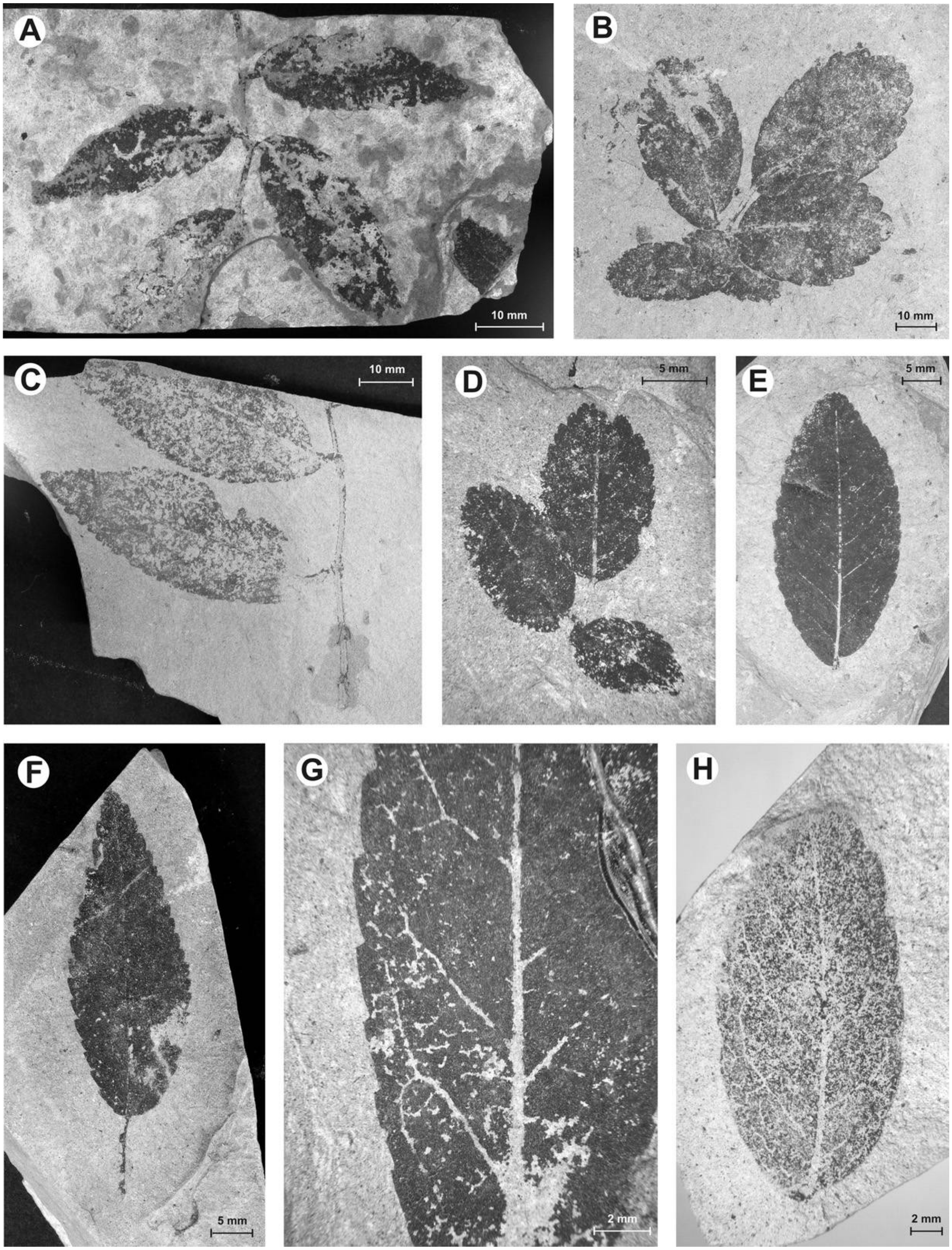

Fig. 4 Leaves and leaflets of fossil *Rosa lignitum* Heer, Seifhennersdorf (Saxony, Germany), Early Oligocene. *A*, Fragmentary large leaf, MMG PB Sf 4067. *B*, Almost complete small leaf, orig. Walther and Kvaček 2007: pl. 14, fig. 6, MMG PB Sf 140. *C*, Fragmentary large leaf, MMG PB Sf 2330. *D*, Fragmentary small leaf, MMG PB Sf 2948. *E*, Single leaflet with rounded apex and asymmetric base, MMG PB Sf 6535. *F*, Single leaflet with acute apex, MMG PB Sf 7257. *G*, Leaflet venation: semicraspedodromous, MMG PB Sf 5764. *H*, Single leaflet: basal third of lamina entire-margined, semicraspedodromous venation, MMG PB Sf 2918.

Table 3

Morphological Characters of Rose Leaflets from Five Fossil Floras in Saxony (Germany) and Northern Bohemia (Czech Republic [CZ]) according to the Leaf Architecture Working Group (1999)

Locality	Seifhennersdorf (Saxony)	Bechlejovice (CZ)	Haselbach (Saxony)	Suletice-Berand (CZ)	Kundratice (CZ)
Age (Ma)	30.44 ± 1.52[a]	26.81 ± 1.34[a]	Earliest Rupelian[b]	28.3 ± 1.4 to 19.8 ± .5[a]	32.75 ± .82[a]
No. specimens	108	1	7	1	12
Laminar area of the leaflet (mm^2; mean; range)	242 (48–617)	213	243 (107–373)	nd	294 (52–624)
Laminar symmetry	Symm./asymm.	Asymm.	Symm./asymm.	Asymm.	Symm./asymm.
Laminar L/W ratio (mean; range)	2.35 (1.5–3.7)	2	2.03 (1.33–2.5)	nd	2.09 (1.64–2.89)
Laminar shape	Elliptic, elliptic-ovate, elliptic oblong	Elliptic	Elliptic, elliptic-ovate, elliptic oblong, ovate	Elliptic	Elliptic, elliptic-ovate, elliptic oblong, ovate
Base shape	Rounded, convex, cuneate-convex	Rounded	Rounded, convex	Rounded, convex	Rounded, convex
Apex shape	Rounded, convex, straight-convex, straight	Convex	Straight-convex	Convex-rounded	Rounded, convex, straight-convex
No. teeth/cm leaf margin	4–6		4–6	5	(3–)4–6(–10)
No. teeth orders	1–2	nd	nd	nd	1–2
Secondary vein category	Semicraspedodromous	nd	nd	nd	nd

Note. Laminar L/W ratio = ratio of length to width of lamina, nd = not determined, symm. = symmetrical, asymm. = asymmetrical.

[a] Stratigraphic ages are after Bellon et al. (1998).

[b] Stratigraphic age is after Standke (2011).

have no access to the wild ancestral forms of tea roses because these species have been influenced by plant breeding for 2000 yr (Krüssmann 1986). *Rosa banksiae* and *R. bracteata* are evergreen climbers. It has been discussed that reticulate joined secondary veins can better cope with damage to the water transport system (e.g., by herbivores) than can open vein systems and that this plays an important role in evergreen and long-living leaves (Roth-Nebelsick et al. 2001). Brochidodromous (secondary veins joined into loops without previous branching) venation has been regarded as plesiomorphic, and craspedodromous venation has been regarded as a derived character state within angiosperms (Hickey and Wolfe 1975; Holländer and Jäger 1994; Roth-Nebelsick et al. 2001). Present data do not support this hypothesis in *Rosa* unambiguously because molecular phylogenetic reconstructions of the genus lack statistical support and especially because basal branches were arranged in contradictory topologies (Wu et al. 2001; Wissemann and Ritz 2005; Bruneau et al. 2007; Koopman et al. 2008). *Rosa persica* was sister to all other rose species in the phylogenies published by Wu et al. (2001) and Wissemann and Ritz (2005). Its leaves are simple and have been interpreted as plesiomorphic, but leaf venation is craspedodromous. However, *R. banksiae* and *R. bracteata*, which have pinnate leaves with semicraspedodromous venation, were sister to *R. persica* and the remaining species of *Rosa* (Wu et al. 2001).

Comparison of Extant Roses with Paleogene Rosa lignitum

With regard to the variability of extant rose species, semicraspedodromous venation was the most remarkable character detected in *R. lignitum*, although it could be detected in only a few samples because of the poor preservation of higher-order venation in fossil leaves (table B2; see also Kvaček and Walther 2004, plate 17/1–2: PRC Be 227; NM G 8398a). As outlined above, this type of secondary vein arrangement was rarely found in extant *Rosa* and was most conspicuously developed in evergreen *R. banksiae*, *R. bracteata*, deciduous *R. helenae*, and deciduous *R. roxburghii*, which are distributed in southeastern China, Japan, and the eastern Indochinese peninsula (Beales 1997; Lingdi et al. 2003; table 4). The leaflet shape of these species also matches that of *R. lignitum*, ranging from elliptic-oblong, elliptic, or elliptic-ovate leaves with rounded to cuneate (often asymmetric) bases and rounded to straight-convex apices (tables 3, 4). Leaflets of *R. lignitum* were mostly elongate, with a mean laminar L/W ratio of ~2 (maximum of 3.7 at the site Seifhennersdorf; table B2), but we also observed a few specimens with roundish leaflets (laminar L/W ratio of ≈1.5; table B2). Our data are not sufficient to explain this shape dimorphism, but leaflet shape also depends on the position of the leaflet in the pinnate leaf (Reichert 2011). The elongate leaflets of *R. lignitum* correspond with the laminar L/W ratios of *R. banksiae*, *R. helenae*, and *R. roxburghii*. *Rosa bracteata* had roundish leaves (laminar L/W ratio of 1.4) and a retuse leaflet apex, but the latter character was not observed in *R. lignitum* (tables 3, 4). The leaflet margin of *R. lignitum* was serrate, with 4–6 teeth/cm leaf margin in one or two orders of teeth, but except for *R. helenae* the leaf margin of extant roses with semicraspedodromous venation was more densely serrated (table 4). Assuming that the fossil rose fruit described as *Rosa saxonica* belongs to the same fossil species, the *R. lignitum* whole plant was also characterized by sepals with entire margins and some small appendages (fig. 1). This character state is observed in the majority of rose species and excludes a close relationship to sect. *Gallicanae* and *Caninae*, both of which have characteristic pinnately divided sepals. Sepals of the fossil fruits persist in an upright position and persist after flowering (fig. 1). Except for *R. roxburghii*, roses with semicraspedodromous venation had reflexed deciduous sepals (table 4), but this character also varies between closely related species of sect. *Caninae* (Ritz and Wissemann 2003; Wissemann

Table 4

Leaf Characters, Ecology, and Distribution of Rose Species with Pronounced Semicraspedodromous Venation

	Rosa banksiae, subg. *Rosa*, sect. *Banksianae*	*Rosa bracteata*, subg. *Rosa*, sect. *Bracteatae*	*Rosa helenae*, subg. *Rosa*, sect. *Synstylae*	*Rosa roxburghii*, subg. *Platyrhodon*
Leaf type	Evergreen	Evergreen	Deciduous	Deciduous
No. leaflets	5	7–9	7	15
Laminar area of leaflet (mm^2; mean ± SD)	101.2 ± 20.3	47.2 ± 11.3	1184.9 ± 115.2	244.1 ± 60.1
Laminar symmetry	Base asymmetrical	Base asymmetrical	Base asymmetrical	Base asymmetrical
Laminar L/W ratio (mean ± SD)	2.91 ± .42	1.44 ± .06	2.12 ± .19	2.8 ± .19
Laminar shape	Elliptic	Elliptic-obovate	Elliptic-oblong	Elliptic-oblong
Base shape	Cuneate	Rounded	Rounded	Cuneate
Apex shape	Straight-convex	Retuse	Convex	Straight-convex
No. teeth/cm leaf margin	10	8	5	8
No. teeth orders	1	1	1	1
Sepal lobation	Entire	Entire	Entire	Entire or lobed
Sepal persistence	Reflexed, deciduous	Reflexed, deciduous	Reflexed, deciduous	Straight, persistent
Fruit surface	Smooth	Smooth	Smooth	Chestnut-like
Distribution	SE China	SE China, S Japan	SE China, Thailand, Vietnam	SE China, Japan
Ecology	Scrub, thickets, valleys, streamsides	Scrub, sandy hills, streamsides, seashores	Thickets, scrub, slopes, streamsides	Mountain forests, thickets, streamsides

Note. Information about distribution and ecology was taken from Lingdi et al. (2003). Laminar L/W ratio = ratio of length to width of lamina, S = southern, SE = southeast.

and Ritz 2007). Interestingly, sepal persistence represents the only distinctive character between the European *R. lignitum* whole plant and the North American Paleogene *Rosa hiliae* Lesquereux (Hably et al. 2000); thus, this character does not contradict a close relationship between these fossil roses. Fruits of *R. saxonica* are more densely prickled than those of *R. roxburghii*. However, this species has a very large number of leaflets (up to 15; table 4), which has not been found in *R. lignitum*. As expected, when the Oligocene fossils were compared with the extant species, the morphological characters of *R. lignitum* did not match exactly with the morphology of any single extant rose species, but we conclude that *R. lignitum* is most similar to extant Southeast Asian rose species.

Paleobiology of Rosa lignitum

The *R. lignitum* whole plant was probably a shrub or a climber. It grew close to lakeshores in volcanic floras because the fossil-bearing diatomite layers were deposited in freshwater lakes of different sizes. The Haselbach leaf assemblages were deposited in abandoned river channels, oxbow lakes, and shallow still waters in swamps (Kunzmann and Walther 2007). Roses may have been growing in riparian forests, in pioneer vegetation on river banks, and in transitional vegetation between azonal riparian forests and zonal mixed mesophytic forests. The preservation and phytotaphonomic data on leaf assemblages of the studied sites suggest parautochthonous taphocoenoses (Kvaček and Walther 1998; Walther and Kvaček 2007); thus, the mother plants of fossil remains (e.g., leaves) were growing nearby the depositional site. Behrensmeyer and Hook (1992) consider an assemblage as parautochthonous if the phytoclasts have been transported away from the death or discard site but have remained within the original habit. The ecology of the morphologically similar Southeast Asian extant roses, which also grow alongside streams, coincide with proposed habitats of *R. lignitum* (table 4). East Asian rose species with semicraspedodromous venation are distributed in mixed broad-leaved deciduous and evergreen forests in the subtropical zone to broad-leaved forests in the transitional tropical zone (Hou et al. 1979). This corroborates the findings of previous studies in which zonal vegetation of the Oligocene volcanic floras of the Seifhennersdorf-Kundratice assemblage and of the lowland floras of the Haselbach assemblage was compared with these extant vegetation types of Southeast Asia (Mai and Walther 1978; Walther and Kvaček 2007). Mixed mesophytic forests, especially from the volcanic floras, were characterized by deciduous broad-leaved trees and the modern Arcto-Tertiary elements (e.g., *Carpinus*, *Ulmus*, *Acer*, *Zelkova*, and *Tilia*), which dominated over the thermophylic evergreen elements (e.g., *Laurophyllum*, *Platanus neptuni*, and *Arecaceae*; Mai and Walther 1978; Kvaček and Walther 1998, 2004). This vegetation represents different stages of transition from the nearly paratropical vegetation of the early to middle Eocene to deciduous temperate forests at the end of the Miocene (Mai 1995) due to the global Cenzoic cooling and the development of pronounced seasonality (Mosbrugger et al. 2005). The close similarity of *R. lignitum* to *R. hiliae* from Paleogene deposits of North America (Meyer and Manchester 1997) suggests a continuous distribution of fossil roses from North America to Europe, which could be facilitated either by the Beringia land bridge, which sundered at 25–15 Ma and 5.5–5.4 Ma, respectively (Milne 2006), or by the North Atlantic land bridge (earlier than 12 Ma; Grimsson and Denk 2007). It seems to be obvious that Southeast Asian roses represent Tertiary relicts surviving in Southeast Asian refugees after Pleistocene cooling because their distribution is rather isolated and exceptional within the Northern Hemispheric temperate genus. However, we do not have anything other than circumstantial evidence to support this hypothesis because phylogenetic reconstructions do not unambiguously support a common and early origin of these species (Wu et al. 2001; Wissemann and Ritz 2005; Bruneau et al. 2007; Koopman et al. 2008). Morphological similarities between *R. lignitum* and Southeast Asian species can also be interpreted as convergent development because brochidodromous venation is more frequent in tropical floras and craspedodromous leaves prevail in northern temperate floras (Bailey and Sinnott 1916). Thus, for future research robust molecular phylogenies of the genus *Rosa* are needed, which will also allow a robust dating of its radiation.

Acknowledgments

We thank M. Will (Johannes Gutenberg University Mainz) and K. Ehlers (Justus Liebig University Gießen) for technical assistance. We thank O. Tietz (Senckenberg Museum for Natural History Görlitz) for very fruitful discussions. We thank two anonymous reviewers for very helpful comments on the manuscript. The work was funded by a grant from the Deutsche Forschungsgemeinschaft to V. Wissemann (Wi 2028-1).

Appendix A

Voucher Information for Herbarium Specimens Analyzed in This Study

All specimens are located in the herbarium V. Wissemann, deposited at Herbarium Gießen (GIE).

Subgenus; section; species; voucher details.

Subg. *Hesperhodos* Cockerell; *R. stellata* Wooton, Germany, Sachsen-Anhalt, Sangerhausen, Europa-Rosarium; leg./det.: V. Wissemann. **Subg. *Hulthemia* (Dumort.) Focke; *R. persica*** Michx., Germany, Niedersachsen, Neuer Botanischer Garten Göttingen; leg./det.: V. Wissemann; 20.05.1997. **Subg. *Platyrhodon* (Hurst) Rheder; *R. roxburghii*** Tratt., Germany, Hessen, Kassel, Rosensammlung; leg./det.: V. Wissemann; 21.05.1997. **Subg. *Rosa*; Sect. *Banksianae* Lindl.; *R. banksiae*** W. T. Aiton, USA, Texas A&M University rose collection (origin China); leg./det.: D. Byrne; 20.06.1998; **Sect. *Bracteatae* Thory; *R. bracteata*** J. C. Wendl., USA, Texas A&M University rose collection R 43-44 (origin China); leg./det.: D. Byrne; 20.6.1998; **Sect. *Caninae* (DC.) Ser.; *R. caesia*** Sm., Germany, Mecklenburg-Vorpommern, Malchin; leg./det.: H. Henker; 26.08.1992; ***R. corymbifera***

Borkh., Germany, Niedersachsen, Groß Schneen, Einzelberg; leg./det.: V. Wissemann; 22.06.1994; ***R. dumalis*** Bechst., Germany, Saarland, Saar-Nahe-Bergland, Otzenhausen; leg./det.: H. Reichert; 27.06.1985; ***R. elliptica*** Tratt., Germany, Sachsen-Anhalt, Heimburg, Ziegenberg; leg./det.: J. Müller; 08.06.1992; ***R. glauca*** Pourr., Germany, Niedersachsen, Göttingen, Alter Botanischer Garten; leg./det.: V. Wissemann; 02.02.1998; ***R. marginata*** Wallr. Germany, Rheinland-Pfalz, Mertesdorf near Trier; leg./det.: H. Reichert; 26.05.1993; ***R. micrantha*** Sm., Germany, Niedersachsen, Groß Schneen, Einzelberg; leg./det.: V. Wissemann; 22.06.1994; ***R. mollis*** Smith, Germany, Mecklenburg-Vorpommern, Hiddensee; leg./det.: V. Wissemann; 12.08.2003; ***R. montana*** Chaix, Austria, Tirol, Vinschgau, Schlanders, Sonnenberg; leg./det.: V. Wissemann; 19.08.1998; ***R. tomentosa*** Sm., Germany, Mecklenburg-Vorpommern, Neukloster-Züsow; leg./det.: H. Henker; 13.07.1987; ***R. villosa*** L., Germany, Schleswig-Holstein, Hollenbeck; leg./det.: V. Wissemann; 10.08.1996; ***R. mangii*** Eigner & Wissemann, Germany, Schleswig-Holstein, Geltinger Birk; leg./det.: V. Wissemann; 10.08.1996; ***R. rubiginosa*** L., Germany, Schleswig-Holstein, Helgoland, dune close to "Friedhof der Namenlosen"; leg./det.: V. Wissemann; 28.03.1996; **Sect. *Gallicanae* (DC.) Ser.; *R. gallica*** L., Germany, Baden-Württemberg, Rottenburg/Neckar, Seebronn; leg./det.: T. Timmermann; 1996; **Sect. *Laevigatae* Thory *R. laevigata*** Michx., USA, Texas A&M University rose collection (origin China); leg./det.: D. Byrne; 20.6.1998; **Sect. *Pimpinellifoliae* (DC.) Ser.; *R. sericea*** Lindl., Germany, Niedersachsen, Göttingen, Alter Botanischer Garten; leg./det.: V. Wissemann; 28.07.1995; ***R. spinosissima*** L., Germany, Schleswig-Holstein, Sylt, south of Klappholttal; leg./det.: V. Wissemann; 13.08.1996. **Sect. *Rosa* (=*Cinnamomeae* DC.); *R. laxa*** Retz., China, Xinjiang, Kongur, Atoinak; leg./det.: M. Richter; 04.07.1996; ***R. majalis*** Herrmann, Germany, Baden-Württemberg, Rottenburg/Neckar, Äuble; leg./det.: C. Ritz; 18.05.2002; ***R. nitida*** Willd., Germany, Niedersachsen, Göttingen, Leonard-Nelson-Strasse; leg./det.: V. Wissemann; 07.05.1997; ***R. pendulina*** L., Germany, Niedersachsen, Göttingen, Alter Botanischer Garten; leg./det.: V. Wissemann; 02.08.1995; ***R. rugosa*** Thunb., Germany, Schleswig-Holstein, Geltinger Birk; leg./det.: V. Wissemann; 10.08.1996; ***R. willmottiae*** Hemsl., Germany, Niedersachsen, Göttingen, Alter Botanischer Garten; leg./det.: V. Wissemann; 28.07.1995. **Sect. *Synstylae* (DC.); *R. arvensis*** Huds., Germany, Niedersachsen, Göttingen, Alter Botanischer Garten; leg./det.: V. Wissemann; 02.08.1995; ***R. helenae*** Rehder & E. H. Wilson, Germany, Hessen, Kassel, Rosensammlung; leg./det.: V. Wissemann; 1996; ***R. multiflora*** Thunb., Germany, Niedersachsen, Göttingen, Alter Botanischer Garten; leg./det.: V. Wissemann; 02.08.1995; ***R. wichurana*** Crép., Germany, Niedersachsen, Göttingen, Alter Botanischer Garten; leg./det.: V. Wissemann; 03.07.1999.

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